

東京帝國大學理學部紀要

第三類 植物學

第二冊 第四篇

---

JOURNAL

OF THE

FACULTY OF SCIENCE

IMPERIAL UNIVERSITY OF TOKYO

SECTION III BOTANY

Vol. II Part 4

---

TOKYO

Published by the University

July 31, 1930



The "JOURNAL OF THE FACULTY OF SCIENCE" is the continuation of the "JOURNAL OF THE COLLEGE OF SCIENCE" published by this University in forty-five volumes (1887-1925), and is issued in five sections:

Section I.—Mathematics, Astronomy, Physics, Chemistry

Section II.—Geology, Mineralogy, Geography, Seismology

Section III.—Botany

Section IV.—Zoology

Section V.—Anthropology

---

#### Committee on Publication

Prof. S. Nakamura, Dean, *ex officio*

Prof. K. Matsubara

Prof. K. Shibata

Prof. N. Yatsu

Prof. T. Kato

---

All communications relating to this JOURNAL should be addressed to the  
DEAN OF THE FACULTY OF SCIENCE, IMPERIAL UNIVERSITY OF TOKYO.



Morphology and Biology of *Glaucidium palmatum*  
 SIEB. et ZUCC. with Notes on Affinities  
 to the Allied Genera *Hydrastis*,  
*Podophyllum* and *Diphylla*

Contributions to Cytology and Genetics from the Departments of Plant-Morphology  
 and of Genetics, Botanical Institute, Faculty of Science,  
 Tokyo Imperial University, No. 92

By

Masao KUMAZAWA

---

With 20 Text-Figures

---

Contents

I.	Introduction . . . . .	346
II.	<i>Glaucidium</i> . . . . .	347
	1. Habit and Morphology of the Adult Plant . . . . .	347
	2. Development of the Seedling . . . . .	349
	3. Anatomy of the Adult Plant . . . . .	352
	4. Anatomy of the Seedling . . . . .	356
III.	<i>Hydrastis</i> , <i>Podophyllum</i> and <i>Diphylla</i> . . . . .	358
	1. Morphology of the Aerial Parts . . . . .	358
	2. Morphology of the Rhizome and Winter Bud . . . . .	359
	3. Vascular Course in the Vegetative and Floral Organs . . . . .	363
	4. Histology of the Aerial Organs . . . . .	367
	5. Histology of the Rhizome and Adventitious Root . . . . .	367
	6. Development and Structure of the Seedling . . . . .	368
IV.	General Remarks and Affinities . . . . .	371
	1. Habit and Geographical Distribution . . . . .	371
	2. Affinities and Conclusion . . . . .	372
V.	Summary . . . . .	377
VI.	Literature . . . . .	379

## I. INTRODUCTION

According to the ENGLER's system now widely accepted, two genera *Glaucidium* and *Hydrastis* form Hydrastideae of Ranunculaceae, but previously PRANTL (1887) established a tribe Paeonieae in Ranunculaceae including these two genera and *Paeonia*. *Glaucidium* and *Hydrastis* are also grouped under Podophylloideae, one of the Berberidaceous sub-families, with other genera such as *Podophyllum*, *Diphylleia*, etc. by WETTSTEIN (1924) and LOTSY (1911), but later TISCHLER (1902) proposed that the two genera *Podophyllum* and *Diphylleia* must represent a separate family Podophyllaceae.

In the work of HIMMELBAUR (1914), it was stated that *Glaucidium* and *Hydrastis* represent Glaucidioidae, while *Podophyllum* and *Diphylleia* represent Podophylloideae; both groups are of Berberidaceae.

Besides, there have been a number of students of taxonomy and morphology treating the affinities of these four small genera (*Glaucidium*, *Hydrastis*, *Podophyllum* and *Diphylleia*) in various ways with different views. This must be due mostly to the floral structure of each genus showing a remarkable difference in order to be grouped in one family. Not only the floral structure of these genera, we have been also much entertained with the morphological and biological points of interest in their vegetative organs as they may be taken to represent abnormal Dicotyledons.

Of the four genera, *Podophyllum* has more species than the other three and was studied more accurately than any of the three in morphological and biological points of view by DICKSON (1889), CITERNE (1892), BASTIN (1894), SCHUMANN (1897), HOLM (1899), TISCHLER (1902), etc.

Both *Glaucidium* and *Hydrastis* are monotypic genera. The structure and biology of *Hydrastis canadensis* L. were studied, to some extent, by a few authors such as SCHUMANN (1897), BOWERS (1891) and POHL (1894), but of *Glaucidium palmatum* SIEB. et ZUCC. no one has yet described in detail. Therefore the present author has attempted to make the study on the very subjects of this interesting endemic genus, and a comparative study of the closely allied genera *Hydrastis*, *Podophyllum* and *Diphylleia* are described in the following paragraphs.



## II. *Glaucidium*

### 1. HABIT AND MORPHOLOGY OF THE ADULT PLANT

This endemic species is distributed in the mountain sides or deciduous forests of central and northern Japan and also of Yezo. The material used in this study was obtained from Mt. Shirane at Nikko.

The habit of this species is almost similar to that of the American allied genera *Hydrastis* and *Podophyllum* which occur, according to HOLM, in association with *Diphylleia*, *Jeffersonia*, *Caulophyllum*, *Actaea*, *Cimicifuga*, etc., all of which are somewhat abnormal Dicotyledons.

*Glaucidium* is a geophilous herb with well-developed rhizome; its erect stem has three or four alternate foliar leaves, the lower two being petiolated and palmate, and these foliar leaves are arranged in  $1/2$  divergence. The stem is terminated by a single flower. In a well-developed plant of which the author has made a careful study, the stem measured 8 mm. in diameter at the base, the lower two leaves having petioles of 6-7 cm. long. The length of the internodes measured from the base upwards 18, 8, 7, and 3 cm. respectively. The uppermost internode, i. e. peduncle was 3 cm. long as shown above and 3 mm. in diameter.

The petiole is almost triangular in cross section and the leaf sheath is not developed except the radical leaf, whose petiole is pretty long.

The elongation of the rhizome is sympodial. When the terminal becomes aerial and dies away, the axillary buds represent the sympodial axis of the rhizome, but there is no regularity in the position of the axillary bud which may become dominant. In such a case the adult rhizome gives an irregular and somewhat massive appearance. The full-grown rhizome is usually 10-15 mm. in diameter, and the scars of vascular strands of the foliar leaves are recognizable. A single foliar leaf with a long petiole or an erect stem with no petiolated radical leaf is seen at the terminal part of the rhizome. The winter bud which conceals an erect stem of the subsequent year is thick, 10 mm. in diameter and 15 mm. in length, but one which encloses a single radical leaf is somewhat slender.

Fig. 1 shows a diagrammatic cross section of the winter bud

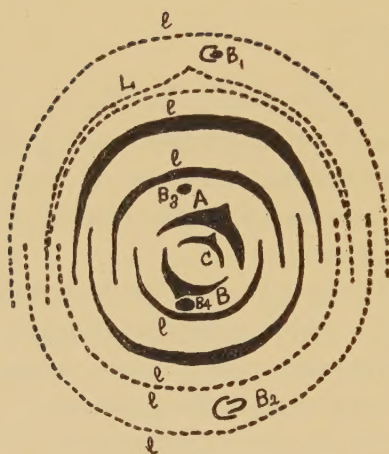


Fig. 1. *Glaucidium palmatum*. Diagram showing the leaf arrangement of a fertile winter bud. l, scaly leaf; L, radical foliar leaf; A, B and C, cauline leaves; B<sub>1</sub>—B<sub>4</sub>, axillary buds.

which conceals an erect stem of the following summer. Letter l denotes the scaly leaves and the broken lines denote scaly leaves (l) or a petiolated foliar leaf (L) now missing. An erect stem is at the centre of the diagram, A, B and C being its cauline leaves. All the leaves show the phyllotaxis of nearly  $1/2$ , but the orthostichies of the cauline leaves deviates a little from that of the scaly leaves. The innermost two scaly leaves embrace the axillary buds (B<sub>3</sub>, B<sub>4</sub>), bud B<sub>3</sub> develops less than B<sub>4</sub>. B<sub>4</sub> may develop, to some extent, after the decay of the terminal erect stem, but

it will never become a floral bud in the course of a few years. As a matter of fact, it requires several years before an axillary bud can produce an erect stem in this species. The four axillary buds B<sub>1</sub>—B<sub>4</sub> are not exactly alternated in their position, but are deviated somewhat.

Prophylls of the axillary bud are arranged laterally to the *Tragblatt* of the mother shoot, as well as the following leaves of the same axillary bud.

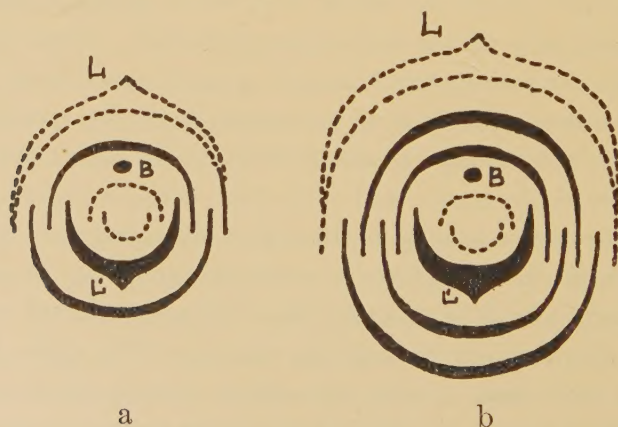


Fig. 2. *Glaucidium palmatum*. Diagrams showing the leaf arrangement of sterile winter buds with two (a) or four (b) scaly leaves. L, L', petiolated radical leaves (L, leaves now missing); B, axillary buds.



Fig. 2 shows a diagrammatic cross section of the sterile winter buds embraced at the base of the petiolated radical leaf. L denotes this petiolated radical leaf of the first year and L' of the subsequent year. It is worthy of note that these two foliar leaves (L and L') are always arranged in the opposite orthostichies of the leaves to each other, and between these two leaves two (Fig. 2, a) or four (Fig. 2, b) scaly leaves of the winter bud are usually found. Only one axillary bud (B) may or may not be recognizable at the axillary part of the innermost scaly leaf. The petiolated radical leaf never embraces the axillary bud in any case.

## 2. DEVELOPMENT OF THE SEEDLING

As the seedlings could be obtained neither in our Botanic Gardens of Koishikawa nor of Nikko, for the seeds seemed incapable of germination in these gardens<sup>1)</sup>, all the seedlings of various stages studied were obtained from the forests of Mt. Shirane, Nikko.

*Seedling in the first year of its germination.* The seeds germinate probably in the early spring and their development of the first year takes place in early summer. Fig. 3 shows a seedling of this condition obtained about the middle of July. The primary root does not yet produce any lateral rootlet, being white or somewhat yellow in colour; the external difference between the primary root and the very short hypocotyl is scarcely noticeable. It is remarkable to see that two cotyledonary petioles fuse and form a tube and also that two cotyledonary laminae fuse at their basal margin. The cotyledonary tube is almost 4 cm. long and elliptical in cross section, being somewhat pale in colour. P shows the position of the dormant plumule

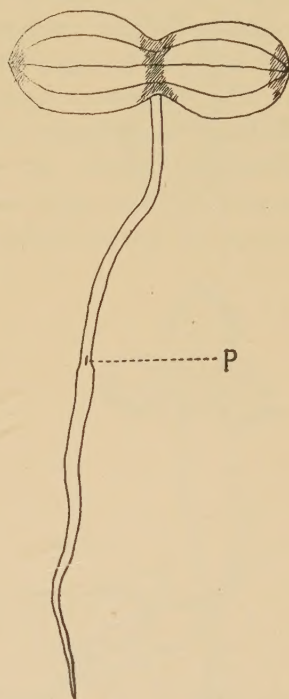


Fig. 3. *Glaucidium palmatum*. Seedling in the first year of its germination. Two cotyledons and cotyledonary petioles are fused respectively. P, plumule. (nat. size)

1) It is unknown to the author whether the condition of those gardens is unfavourable for the germination or whether the seeds require a comparatively long dormant period before germination. Even in their native place very small numbers of the seedlings were found.

which is enclosed by the tube; any aerial organ, except the cotyledons, does not appear in the first year of its germination. Cotyledonary lamina is oval or elliptical in shape without any serration, being 17 mm. long and 13 mm. wide. No epidermal hairs are observed either on the lamina or petiole. In fact, the assimilating organ of the seedling represented only by the cotyledons and the plumular dormancy in the first year of the germination are usually not found in Ranunculaceae or in other Dicotyledons with a few exceptions.

Assimilated material, i. e. starch, is stored in both subterranean hypocotyl and root for the production of the foliar leaf in the following year.

Fig. 4 shows a cross section through the basal cotyledonary tube in which three primordial leaves are seen. These primordia are the scaly leaves, arranged alternately in the phyllotaxis of nearly  $1/2$ , but the foliar leaf of the next year is not yet recognizable.

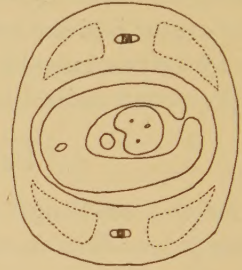


Fig. 4. *Glaucidium palmatum*. Cross section of the basal part of the cotyledonary tube. (ca.  $\times 17$ )



Fig. 5. *Glaucidium palmatum*. Seedling in the second year of its germination. Two adventitious roots are produced from the young rhizomal part. (nat. size)

After the decay of cotyledonary tube, the first scaly leaf lies unprotected during the winter in the ground. The leaf immediately succeeding the cotyledons is scaly in this species, as it is rarely the case in the dicotyledonous seedlings; this subject will be explained later.

*Seedling in the second year of its germination.* The seedlings of this stage as obtained (Fig. 5) bear one petiolated foliar leaf and three scaly leaves, the outermost scale often missing. The internodes of these leaves are very short so as to form a young rhizomal part, whose diameter increases slightly, and from this part a few adventitious roots and



dormant axillary buds may appear. The petiole of the first foliar leaf is 4 cm. long, about 1 mm. wide, somewhat triangular in cross section; the lamina is three-lobed, having unicellular hairs at the margin as in the adult leaf. On account of being enclosed by the basal part of the petiole, one or two scaly leaves may or may not be observed. The hypocotyl and the main root do not increase their diameter and they are uniformly brown in colour; the latter produces some lateral rootlets.

*Seedling in the third and subsequent years of its germination.*

Fig. 6 shows the third year seedling which has also a single foliar leaf and three or four scaly leaves, and is almost similar to that of the second year, but the foliar leaf is larger and the root has developed more lateral rootlets. The young rhizome is monopodial and also very small, more or less creeping.

In the seedlings of the subsequent years, the same morphological features are observed; the rhizome is very short and slender, representing a monopodium. Even in the seedling which seems to be in the sixth year of its germination, the rhizome is 1.8 cm. long and 3 mm. wide with five to seven dormant buds and is usually monopodial, when no accident occurs. In the seedling, the petiole of foliar leaf is 12 cm. long and 2-3 mm. wide, but neither hypocotyl nor main root usually persists at this time.

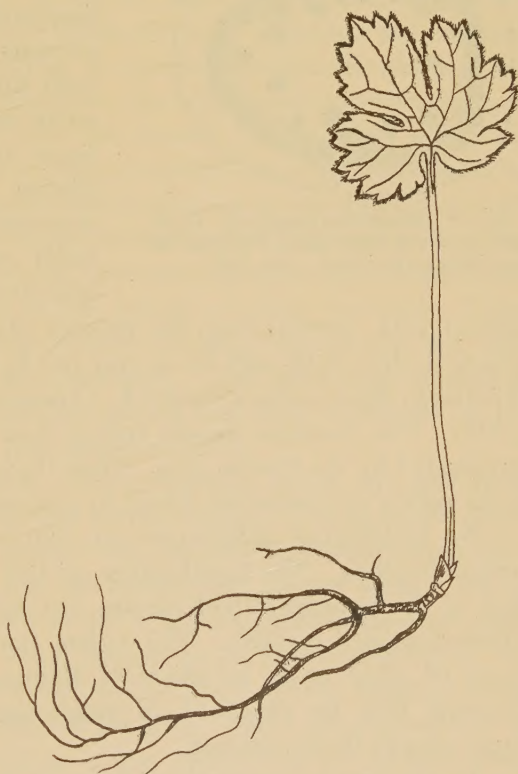


Fig. 6. *Glaucidium palmatum*. Seedling in the third year of its germination. (slightly enlarged)



Judging from this observation, the development of the seedling of *Glaucidium palmatum* is extraordinarily slow, and in the natural condition it seems to be difficult for this herb to produce an erect stem terminated by a single flower at least within ten years after its germination.

### 3. ANATOMY OF THE ADULT PLANT

*Erect Stem and Peduncle.* The aerial stem (Fig. 7) is solid and the vascular strands are arranged nearly in two rings; the strands of the

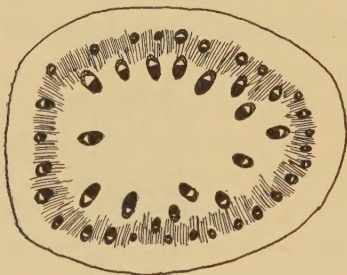


Fig. 7. *Glaucidium palmatum*. Cross section of the erect stem, showing the vascular arrangement. (ca.  $\times 6$ )

outer circle are more numerous and small in size, and are protected at the base of the stem by an interfascicular fibrous cylinder<sup>1)</sup> which consists of three or four layers of cells with lignified walls. The vascular strands of the inner circle are large in size and free from the fibrous cylinder. Besides this common fibrous cylinder, each vascular strand is provided with a well-developed fibrous arc on the

phloem side, surrounding the phloem part only, but slightly lignified cells with thin walls may be or may not be observed on the xylem side as found in *Ranunculus sceleratus* L. (Anemone Type of the author (1930); p. 312). The vascular strands reduce their phloem, and are practically surrounded by the fibrous ring, when they are situated most externally in the cortex as commonly found in monocotyledonous bundles.

No histological differences are found between the medullary and normal bundles. The lignification of the xylem occurs at the same time in the bundles of both circles, but the xylem of the inner circle is rather elongated radially. The xylem does not show the typical V-shape of other usual members of Ranunculaceae, and the secondary elements may be produced in small amounts. The endodermis or starch sheath is not distinct.

In the lowest internode of the erect stem, the vascular strands are usually 35–50 in number, while in the peduncle they are reduced to about 30 and are scattered irregularly in the fundamental tissue (Fig. 15, A). In the older peduncle with mature seeds, each vascular strand is

1) HIMMELBAUR (1914; p. 771) did not observe this fibrous cylinder in the materials studied by him.



surrounded by an individual fibrous sheath, and also both primary ray and pith are usually occupied by the cells with lignified thick walls. Epidermis and cortex often shrink and lose their cell contents. It is noticed in the older peduncle that the xylem of the medullary bundles is much concave towards the phloem side forming a V-shape, not like the xylem of the peripheral bundles or that of the stem bundles.

*Course of the Vascular System.* Medullary bundles are observed in the peduncle, the erect stem and the petiole, but not in the rhizome. Their courses were studied by tracing them in numbers of cross sections, but owing to its complexity only the following account could be given as far as the result of the present study is concerned.

Medullary bundles, five to six or more in number, are clearly observed in the floral receptacle where the four perianths are inserted. The vascular strands, belonging to a perianth, enter into three or five different points of the floral receptacle, the middle one penetrating much more deeply into the pith than the lateral ones. These medullary bundles thus formed fuse with the peripheral or other bundles in the third internode. In the material described in the foregoing page (p. 347), the uppermost cauline leaf without petiole sends trilacunarly into the medullary part of the stem three large trace strands, from which a few very minute strands depart at the points of their entrance. These minute strands run downwards without bending inwards and fuse with other peripheral strands in that internode. The three large strands go down through the following two internodes and bend outwards in the third internode, fusing with the peripheral ones.

The next foliar leaf below, without petiole, sends five leaf trace strands, except several minute ones corresponding to those of the upper leaf described above. Among these five strands, the middle three bend towards the pith and go down to the lowest part of the erect stem in the pith, while the lateral two descend in the peripheral parts and then fuse, in some distances, with other strands in the lowest internode.

Petiolated foliar leaves have nine or more strands inserted to the stem; some of them turn inwards to the pith, while others descend in the peripheral parts, and within a few millimeters all the medullary bundles in the stem become peripheral at the basal parts of the erect stem; thus a usual vascular arrangement of the rhizome is formed as its result.

*Rhizome.* Both interfascicular and intrafascicular cambium are very active, the former producing seriated parenchymatous cells on both radial sides, while the latter produces xylem elements internally



and phloem elements externally. Xylem elements consist of vessels, parenchymatous cells and fibres or fibre-tracheids. Fibres or fibre-tracheids appear in a group, occupying some parts of the xylem (Fig. 8, black part) with no other elements. Phloem elements are represented by radially depressed cells, but no further differentiation is recognized.

By the early development of the secondary tissue, both epidermal and outer cortical layers peel off even in the youngest rhizome; then,

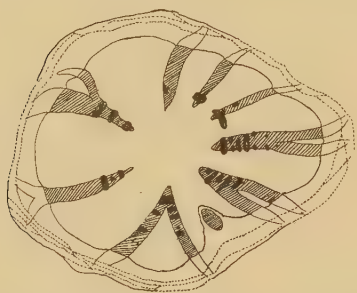


Fig. 8. *Glaucidium palmatum*. Diagram showing the cross section of the rhizome. Broken lines, pseudodermis; black area, grouped fibres or fibre-tracheids in xylem. ( $\times 5$ )

for protecting purpose, the lignification of the radial walls takes place in a tangential layer which consists of a row of the uniseriate cells (Fig. 8, broken lines). These modified seriate cells are derived from those of the cortex or even of the phloem, their radial walls being lignified quite secondarily; thus the layer of the uniseriate cells shows the endodermal appearance. When this layer is destroyed, new layers become differentiated more internally,

sometimes in the part of the secondary phloem. Three or more layers under consideration are often developed, being separated from each other. It may, therefore, appear as a kind of a reduced form of the peridermis, but it is a single layer of the cells caused by the modification of the cell walls of pre-existing tissue and is not derived directly from the secondary meristem such as cork cambium. The elements of the layer do not divide throughout their life. DOULIOT (1889) described and figured the cell layer which has the same features with the layer above described in various genera of Dicotyledons, and he called the layer as "assise plissée", but the layer described by him differentiates in the peridermis; thus the two kinds of the layers are different in their development. Therefore, the present author proposes to name the layer dealt with in this paper as "pseudodermis". The layer is regarded as a kind of exodermis, but it is very remarkably manifested in the rhizome of this species. The function is similar to that of the cork layer and of exodermis.

*Leaf.* The vascular strands in a petiole are less than 30 in number, one to six of which are medullary, the xylem being abaxial. Prior to



the petiolar insertion to the stem or rhizome, the ventral vascular strands fuse to the medullary ones and then to the dorsal ones. The petiolar structure is similar, in general, to that of the stem, but a lysigenous space is often observed at the centre, being irregular in shape. Small bundles in the midrib, one to three in number, have abaxial xylem and are developed later.

Stomata are not found on the upper epidermis of the lamina, and the mesophyll consists of layers of seven to ten cells, but no differentiation takes place between the palisade and spongy tissues. The chlorophyll-bodies are uniformly distributed in all cells.

*Root.* The main root is diarch and primary xylem does not meet at the centre. The cambial ring produces a portion of the secondary xylem elements between the two strands of the primary xylem. The Casparian strips are easily distinguished. The cambial ring of the adventitious root which is tetrarch or pentarch produces the secondary elements on both sides, and the parenchymatous cells are increased at the part opposite to the primary xylem, but in some cases fibres or fibre-tracheids in xylem may be produced at that part. The vessels, somewhat in radial rows, are situated at the middle part of each secondary xylem group. The epidermal and cortical cells may lose their contents, but do not usually peel off.

Endodermal cells are thin-walled.

Rootlets of the second order are rather simple in structure, being similar to that of the main root.

*Floral Organs.* The perianths are four in number and are usually trilacunar or sometimes pentalacunar organs, forming the medullary bundles as already mentioned. The vascular course in the floral receptacle is extraordinarily complex in this genus. Stamen traces occur from the cortical bundles which are the continuation of the receptacular bundles. If a cortical strand is traced by the cross section from the base of the floral receptacle upwards, it migrates more and more peripherally, producing several traces of the stamens. The stamens in a flower are numerous and each of them is provided with a single strand as usual. Such a complicated feature was not seen in any other species of Ranunculaceae and of Berberidaceae studied by the author.

The two opposite carpels are provided with three strands and are of unilacunar origin. Fig. 9 is a diagrammatic cross



Fig. 9. *Glaucidium palmatum*. Diagram showing a cross section of the upper part of the floral receptacle. Explanation in text. (ca.  $\times 20$ )

section through the top of the floral receptacle in a rather young stage, showing the vascular arrangement. Two carpels are supplied with three strands  $l_1$ ,  $M_1$ ,  $l_1$  and  $l_2$ ,  $M_2$ ,  $l_2$  respectively. The strands A and B ascend slightly upwards and disappear soon, hence it may not be wrong to say that these strands may be abortive carpelar traces.

The histological structure of the pericarp is similar to that of *Hydrastis* studied by POHL (1894).

#### 4. ANATOMY OF THE SEEDLING

The vascular strands of the seedling in the first year of its germination were traced from the base upwards by making the cross section, and their behaviour was studied as follows (Fig. 10).

Two hypocotylar phloem strands divide into three, thus forming six phloem strands ( $p_1-p_3$ ,  $p_1'-p_3'$ ). Then a pair of the new xylem strands differentiates facing to the phloem strands  $p_2$  and  $p_2'$  and forming a pair of the collateral plumular bundles. In the time of exit of traces of the first and second leaves, four plumular strands A-D are produced from a pair of the collateral bundles mentioned above. Each of the exarch xylem strands of the root system elongates tangentially and enters into a cotyledonary petiole associated with two phloem strands  $p_1$  and  $p_1'$  or  $p_2$  and  $p_2'$ . Therefore the xylem of the dormant plumular strands have no direct connection with the xylem of the root system of the seedling in the first year of its germination. This may be due, in all probability, to the fact that the cotyledons alone perform the function of the assimilat-

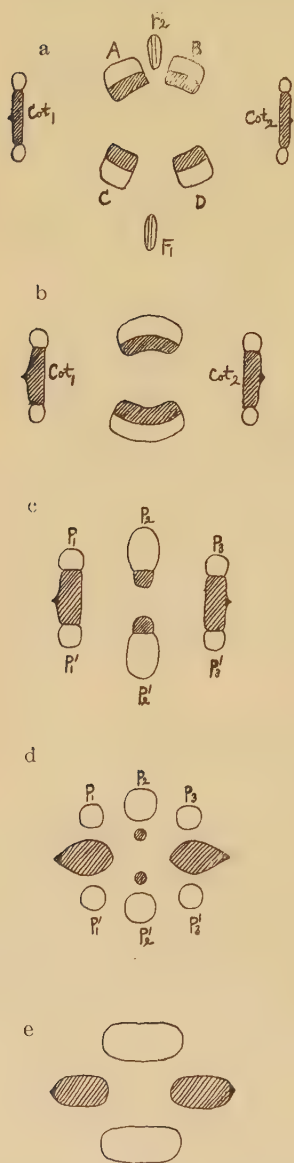


Fig. 10. *Glaucidium palmatum*. Diagrams showing the hypocotylar vascular behaviour. a, cross section of epicotyl; e, that of hypocotyl; b, c, d, sections between a and e; shade, xylem-area; black, protoxylem. Explanation in text.



ing organ during that stage and that the cotyledonary traces are only the conducting passages for the materials.

But in the second year of its germination, xylem of the plumular bundles is directly connected to that of the root system, i. e. to the secondary xylem which developed on the inner side of the phloem strands of the root.

Fig. 11 shows the diagrammatic vascular course of a seedling in the second year of its germination. The first scaly leaf is supplied with only a single strand in all the individuals studied, but the second scaly leaf is supplied with three strands except in a case shown in Fig. 11. Generally, three strands enter into a seedling leaf, each forming a gap of its own on the central cylinder, but often the lateral two are not observed in the case of the scaly leaves.  $M_1-M_4$  in the figure indicate the midribs of the scaly leaves.  $M_6$  and  $M_7$  are also scaly leaves being enclosed by a petiolated leaf ( $M_5$ ) of this year. An axillary bud  $b$  is seen at the node of  $M_4$ .

In the first year of the seedling, the epidermis and a subepidermal layer of the hypocotyl consist of the cells with lignified walls, being brown in colour, but do not peel off usually. The hypocotylar central cylinder is elliptical in cross section, rather elongating in the direction of both xylem. An active cambium is clearly recognized on the inner side of the phloem, but it does not cause the radial thickening of the central cylinder.

In the second year, the hypocotyl increases greatly its diameter by producing the 7-8 cell layers of xylem elements in the radial direction,

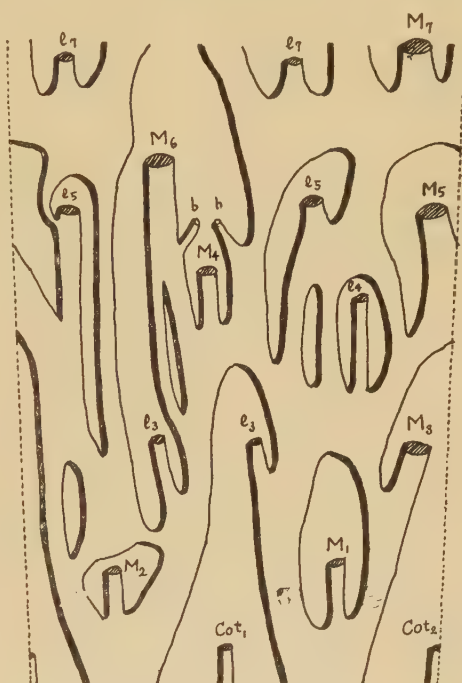


Fig. 11. *Glaucidium palmatum*. Diagram showing the vascular course in the seedling of the second year of its germination.  $Cot_1$ ,  $Cot_2$ , cotyledonary traces;  $M_1$ ,  $M_2$ , ..., midrib strands to the first, the second and the following leaves;  $l_3$ ,  $l_4$ , ..., lateral strands to the third, the fourth, and the following leaves;  $b$ , strands to an axillary bud.

and a lignified cortical layer, i. e. pseudodermis is made and then exposed.

The cotyledonary tube consists of thin-walled cells, having lysigenous spaces in the fundamental tissue. A cotyledonary trace is tangentially elongated in cross section through the tube, phloem being situated at both ends of the tangential elongation, xylem being at the middle.

The remains of the centripetal xylem of the root system is still recognizable at the lower part of the cotyledonary tube.

### III. *Hydrastis*, *Podophyllum* AND *Diphyllia*

The author has described morphology and biology of *Glaucidium palmatum* SIEB. et ZUCC. in the foregoing paragraphs. Now the closely allied genera *Hydrastis*, *Podophyllum* and *Diphyllia* must be studied in order to understand both the affinities of *Glaucidium* to these genera and the systematic position of four small genera cited just above.

#### 1. MORPHOLOGY OF THE AERIAL PARTS

*Hydrastis*. *Hydrastis canadensis* L., a monotypic genus and species from North America, was studied with the fresh material cultivated in our Botanic Garden. The general appearance is somewhat similar to *Glaucidium*, but it is more slender. The aerial stem is 17–20 cm. high and is terminated by a single flower as in *Glaucidium*. Two cauline leaves are alternate and are arranged in  $1/2$  divergence, the lower one having a petiole of 4 cm., the upper one no petiole. Lamina is palmate and 5–7 lobed.

*Podophyllum*. *Podophyllum* contains probably more than four species, of which *P. peltatum* L. was studied with the plant cultivated also in our Botanic Garden. The stem has two cauline leaves each with a long petiole, but the two petioles are quite opposite at the same level on the stem. The flower with a short peduncle lies between the two petioles. Lamina is peltate and 5–9 lobed. According to the descriptions of other authors, the mode of leaf attachment is similar to that of the former species, even in the case of *P. pleianthum* HANCE; in which, however, the inflorescence is cymose and flowers are 5–6 in number. The cauline leaves of *P. Emodi* WALL. and of *P. versipelle* HANCE are not inserted opposite each other at the same level, but are alternate as in *Glaucidium* and *Hydrastis*. They are peltate. The inflorescence of *P. versipelle* is cymose, flowers being about 20 in number.



*Diphylleia*. *Diphylleia* consists of two species, *D. cymosa* MICHX. and *D. Grayi* FR. SCHMIDT, both with two cauline leaves, the arrangement of which is similar to that of *Hydrastis*. In these species the inflorescence is also cymose; the leaves are peltate. *D. Grayi* was collected from Mt. Shirane at Nikko, and was examined in this study.

In short, all these genera have usually two cauline leaves which are alternate or opposite and are arranged in 1/2 divergence. The erect stem has no petiolated radical leaf. The inflorescence is simple or cymose.

## 2. MORPHOLOGY OF THE RHIZOME AND WINTER BUD

*Hydrastis*. The rhizome of *Hydrastis* has the same appearance as that of *Glaucidium*. It is sympodial, but not of a simple sympodium which elongates horizontally. The fertile winter bud is rather small in size and is enclosed by three scaly leaves in the examples examined by the author. The scaly leaves are arranged in 1/2 divergence, each embracing an axillary bud, the innermost axillary bud being the largest. The axillary bud does not produce an erect stem in a few years as in *Glaucidium*. The prophyll of axillary bud is inverted dissimilar to that of *Glaucidium* in which it is lateral.

*Podophyllum* and *Diphylleia*. The rhizomes of these genera are morphologically different from either *Glaucidium* or *Hydrastis*. In *Podophyllum* and *Diphylleia*, the main axis of the rhizome is replaced by an axillary bud in each year; the sympodium elongates quite horizontally in the same direction as the older part as if it were the main axis itself. It is worthy of note that the largest axillary bud representing the sympodial axis is always constant in its position in the winter bud, and that the axillary bud becomes aerial after passing two winters. In other words, the sympodial rhizome elongates in one horizontal direction, producing an erect stem every year. The scars of the erect stems are closely arranged with one another in the species of *Diphylleia* and in *Podophyllum Emodi*.

Although morphological studies of the winter bud of *P. peltatum* had been made by SCHUMANN (1897), HOLM (1899) and TISCHLER (1902), the diagrammatic cross sections of the fertile winter bud figured by them (compare Fig. 13, A, B, C) are somewhat contradictory to each other. Nevertheless the points coincident among them are as follows:

1) An erect stem<sup>1)</sup> terminated by the flower is protected by five (SCHUMANN, TISCHLER) or six (HOLM) scaly leaves.

---

1) According to SCHUMANN and TISCHLER, the terminal of the winter bud is

2) The first and the second scaly leaves of the winter bud, which conceals an erect stem of the next growing season, are alternate to each other regularly.

3) The third, the fourth and the fifth scaly leaves are also alternate to each other, but they turn nearly  $45^\circ$  (HOLM, TISCHLER) or  $90^\circ$  (SCHUMANN) from the first and the second leaves.

4) Each of the third and fourth scaly leaves embraces an axillary bud; the latter embraced by the third scaly leaf elongates, without exception, representing a horizontal sympodium of the rhizome; the other bud is dormant.

The author studied a number of winter buds of *P. pellatum* cultivated in the Medicinal Plant Garden of the Tokyo Hygienic Laboratory at Kasukabe<sup>2)</sup> and in our University Botanic Garden at Koishikawa.

The cross sections of buds were made from the top downwards. Diagrams A and A' in Fig. 12 show the leaf arrangement in the upper parts of two fertile winter buds respectively. Both consist of five<sup>3)</sup> scaly leaves  $l_1-l_5$ ,  $l_1$  being decayed; the outer two ( $l_1-l_2$ ) are not laterally situated, but turned nearly  $45^\circ$  in A, about  $20^\circ$  in A'.  $l_3-l_5$  are quite regularly or almost regularly alternate, but they turned about  $45^\circ$  from  $l_1$  and  $l_2$  in both buds. The opposite cauline leaves turn from the innermost scaly leaves about or less than  $45^\circ$ . Therefore the arrangement of the scaly leaves is almost similar to the diagrams given by HOLM (Fig. 13, B) and TISCHLER (Fig. 13, C).

Diagrams B and B' in Fig. 12 show the cross sections cut through more basal parts of the winter buds than in the cases of A and A'; diagrams A and B were made from one and the same bud, A' and B' from another. Unexpectedly the author found in B and B' that the arrangement of scaly leaves show no more the  $1/2$  phyllotaxis, but the leaves are all spirally arranged almost in  $2/5$  divergence<sup>4)</sup>. It seems that these diagrams, illustrating the basal cross sections of buds, must be an indication of the typical arrangement of the leaves of winter

---

represented by an erect stem, while according to HOLM it is dormant and an erect stem is axillary. The present author supports the opinion of the former authors by the result obtained in his own study.

2) The author thanks the director of the Garden for his facilities for sending valuable materials.

3) Winter buds with six leaves, described by HOLM as normal, were also found in the present study, but they were quite uncommon.

4) But in the diagram B, the scales  $l_1$  and  $l_2$  seem to be nearly alternate.



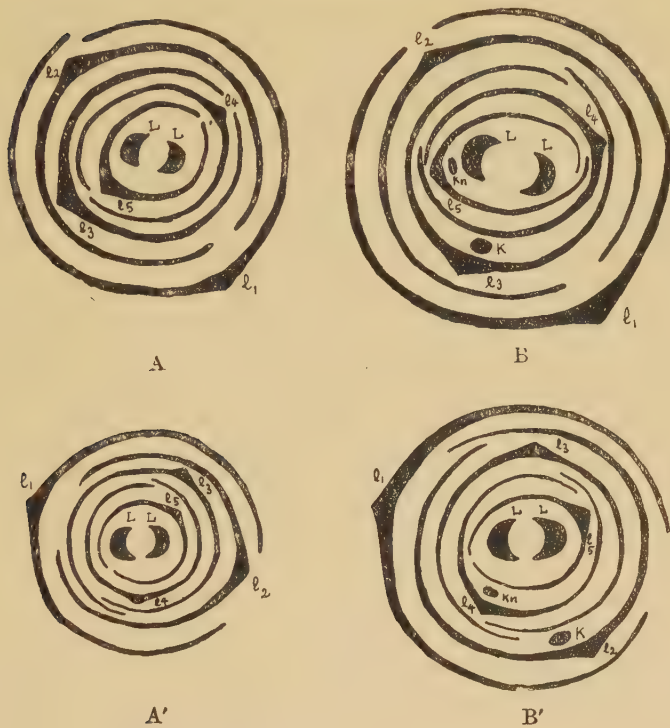


Fig. 12. *Podophyllum peltatum*. Diagrams showing the leaf arrangement of two fertile winter buds. A and A', leaf arrangement at the top of the two buds; B and B', at more basal part of the two buds than A and A' respectively; l, scale leaf; L, opposite cauline leaves; K, dominant axillary bud which represents the sympodial axis; kn, dormant axillary bud.

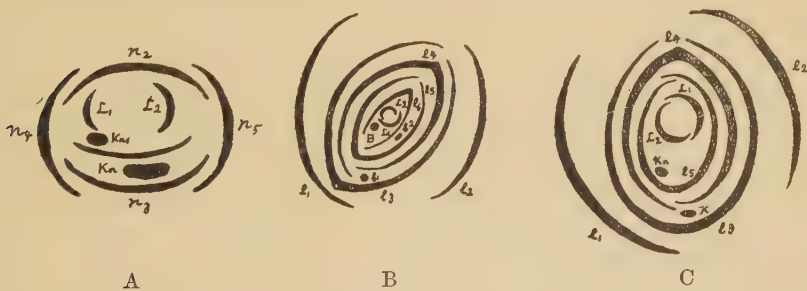


Fig. 13. *Podophyllum peltatum*. Diagrams of cross sections of the fertile winter buds, given by early authors: A, by SCHUMANN; B, by HOLM; C, by TISCHLER. These three diagrams were reproduced from TISCHLER's paper.

buds, and the arrangement of the scaly leaves which are visible in the upper cross sections (A, A') may not be showing the real phyllotaxis, but may be a modified one, and further that the diagrams given by SCHUMANN, HOLM and TISCHLER might be, according to the author's

presumption, made from such sections. Although several of the buds examined were different from one another in respect to the arrangement of leaves and to the position of axillary buds, the present author observed that the scaly leaves of fertile winter buds are usually<sup>1)</sup> arranged in  $2/5$  divergence in the case of *Podophyllum peltatum* cultivated in this country; and he disagrees with the views of other authors who believed the  $1/2$  phyllotaxis for the following reasons:

1) In the basal cross sections of the bud, the leaves are arranged nearly in  $2/5$  divergence, although at the higher level they change and are alternate as described above. The basal cross section shows rather exactly the topography of the real foliar attachment upon an axis.

2) The cauline leaves deviate a little from other scaly leaves in their arrangement, and this deviation can not be explained by the  $1/2$  phyllotaxis. In the author's observation (Fig. 12) and also in the diagrams of HOLM (Fig. 13, B) and TISCHLER (Fig. 13, C) one of the opposite cauline leaves turns about  $2/5$  of a circle from the innermost scaly leaves.

3) The axillary buds<sup>2)</sup> in a winter bud are mostly extraaxial in the diagrams given by the early authors, while they are not almost extra-axial in the present observation. The result of the present observation seems more acceptable than that of the early authors.

4) The winter bud of the most closely related genus *Diphylleia* has also the phyllotaxis of  $2/5$  divergence.

The sterile winter bud consists of five, rarely four or six scaly leaves, the outer one or two of which are often decayed. The arrangement of scaly leaves and the position of axillary buds are similar to those of the fertile winter buds.

*Diphylleia*. Both species of *Diphylleia* are similar to one another regarding morphology of the winter buds and are closely related to *Podophyllum peltatum*. The bud of *D. cymosa* consists, according to TISCHLER (1902; p. 118, Fig. 28), of five scaly leaves and of two or three axillary buds; the outermost bud, embraced by  $l_3$ , represents the sympodial axis of the subsequent year, the buds embraced by  $l_4$  or  $l_5$  are dormant.

The winter bud of *D. Grayi* (Fig. 14) observed by the author has

---

1) In a few buds the scaly leaves seemed to be arranged alternately even in the basal cross section.

2) These axillary buds are two in number and are embraced by  $l_3$  and  $l_5$  respectively in the material observed by SCHUMANN and TISCHLER, but they may be embraced by other scaly leaves as found in one of our examples (Fig. 12, B'; K). The outermost axillary bud K represents always the sympodial axis of the rhizome.



also five scaly leaves and usually two axillary buds. The innermost bud is dominant and is embraced by  $l_4$  in this species, but another dormant bud is embraced by  $l_2$  instead of  $l_4$  of *D. cymosa*.

The phyllotaxis is  $2/5$  in both species.

The prophyll of the axillary bud is inverted in *Podophyllum* and is lateral in *Diphylleia*.

In short, *Glaucidium* and *Hydrastis* are clearly distinguished from *Podophyllum* and *Diphylleia* by the mode of rhizomal elongation and phyllotaxis of scaly leaves.

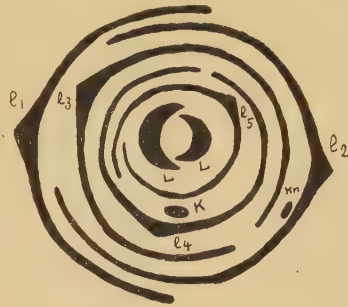


Fig. 14. *Diphylleia Grayi*. Diagram showing a cross section of the fertile winter bud. Explanation as in Fig. 12.

### 3. VASCULAR COURSE IN THE VEGETATIVE AND FLORAL ORGANS

*Hydrastis*. In the lowest internode of the erect stem (Fig. 17, B), 25–30 strands are arranged in two imperfect circles, 4 or 5 strands among them being situated in the medullary region, forming an inner circle, while the peduncle has ten or more strands which are arranged in a circle. The upper cauline leaf sends three or more leaf trace strands into the stem; these strands enter to the vascular circle of the stem and descend through the first internode, and then they bend inwards becoming medullary strands in the second internode. Therefore medullary bundles are visible only in the lowest internode of the erect stem. The petiole is provided with 12–15 vascular strands, a few of which are medullary.

In the floral receptacle, about eight vascular strands are observed at its lower level, and no cortical or medullary bundles occur in the floral axis of this species. The perianth, the stamen and the carpel are all unilacunar organs. The stamen trace travels outwards quite radially soon after it departs from the central cylinder of the flower.

The vascular course of *Hydrastis* is more simple than that of *Glaucidium*, in which medullary bundles are visible from the floral receptacle to the base of the erect stem, while in *Hydrastis* they occur only in the lowest internode.

*Podophyllum*. The cross sections of the peduncle and of the erect stem show a quite monocotyledonous appearance in *P. peltatum*, the

bundles being irregularly scattered in the pith. In the lowest internode of the erect stem (Fig. 17, C), 60–70 strands are visible, of which

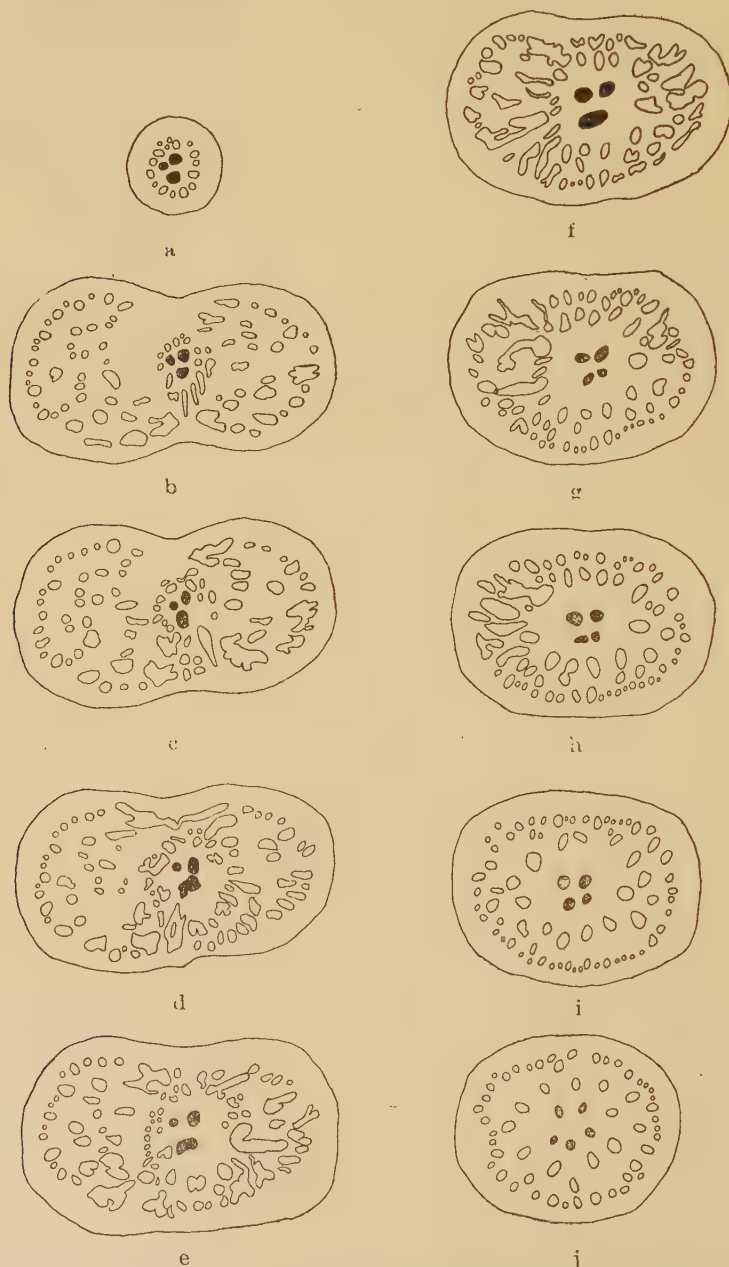


Fig. 15. *Podophyllum peltatum*. Successive cross sections of the stem to show the course of the *stammeigen* bundles (black in the figures). a, lower part of the peduncle; b-h, the level where two opposite petioles insert; j, basal part of the stem. ( $\times 4$ )



about 30 are medullary. The peduncle has less than 20 strands which constitute mostly two circles, the inner one consisting of large strands, 3-6 in number. The petiole has 5-7 medullary bundles in the centre and is almost similar to that of *Glaucidium*.

The vascular course of *P. peltatum* was described by TISCHLER (1902, p. 109) to some extent, who showed that the medullary bundles are leaf trace strands in their origin and the peripheral bundles of the peduncle are connected to those of the petiole. But the author has found an interesting fact which escaped TISCHLER's attention: 4-5 vascular strands situated at the centre of the pith of the peduncle descend to the base of the erect stem, occupying just the centre of the pith without connecting to any bundles (Fig. 15, black bundles). They are not the leaf trace strands<sup>1)</sup> in their origin and are so-called *stammeigen*, and have never been expected in this genus by authors such as DE BARY (1877, p. 259), VAN TIEGHEM (1884, p. 747), SOLEREDER (1899, p. 53) and TISCHLER (1902, p. 109). Tracing these cauline bundles upwards, the author found them bending outwards at the floral receptacle and passing into each external perianth as its midrib; hence there are no medullary bundles at the level higher than the level where the perianths have already departed.

Perianths situated rather externally are trilacunar in their vascular origin, while the internal ones are usually unilacunar and trilobed, and their vascular strands do not bend into the pith of the receptacle.

In the filament and connective of stamens, two vascular strands, one is in inverted orientation, are arranged in the radial plane, xylem of these strands being face to face. This feature is never found in other three genera, whose stamens are provided with a single vascular strand.

*Diphylleia*. The vascular topography in the cross sections of the aerial axis (Fig. 17, D), of the peduncle (Fig. 16, B), and of the petiole of *D. Grayi* is similar to that of *P. peltatum*; 4 or 5 strands

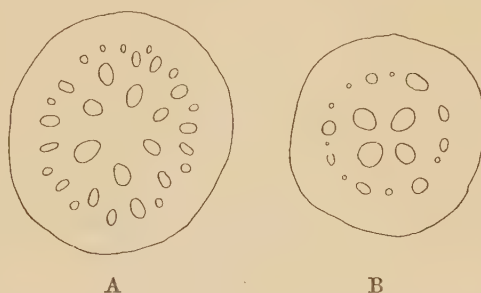


Fig. 16. Cross sections of peduncles, showing the arrangement of medullary bundles. (ca.  $\times 8$ )

A, *Glaucidium palmatum*  
B, *Diphylleia Grayi*

1) WORSDELL (1908; p. 673) suggested this fact in the same species, but the behaviour was not traced in detail.

at the innermost part of the pith of stem base are cauline bundles, and they have their origin in the medullary bundles of the peduncle as observed in *P. peltatum*. But in *D. Grayi* most of these strands are connected with the peripheral bundles which descend from the peduncle at the upper node or with some trace strands of the upper leaf at the lower node. At the basal part of the floral receptacle, medullary bundles are reduced to three or four in number (Fig. 16, B), but are extraordinarily large in size in comparison with the peripheral bundles which are arranged in a circle, as observed in some monocotyledonous peduncles (GATIN; 1920). These bundles, each dividing into two or three parts, run outwards into the ordinary vascular circle at the higher level. All the perianths are unilacunar organ and trilobed.

Now, comparing the result of the present studies on these four genera, the author observed that the medullary bundles are developed in the aerial stem (Fig. 17), arranged nearly in one circle in *Glaucidium* and *Hydrastis*, while in *Podophyllum* and *Diphylleia* they are quite irregular in arrangement. In the former two, they are leaf trace strands, while

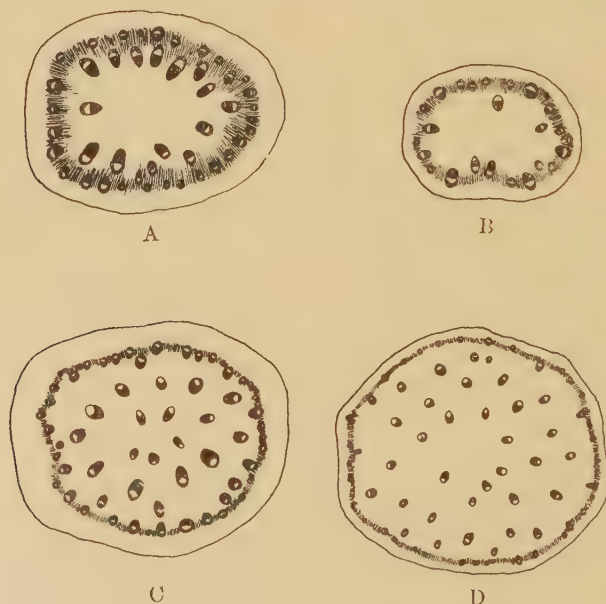


Fig. 17. Cross sections at the lower part of the erect stems, showing the vascular arrangement. The interfascicular fibrous cylinder is shown by the shade. (ca.  $\times 5$ )

A, *Glaucidium palmatum*

C, *Podophyllum peltatum*

B, *Hydrastis canadensis*

D, *Diphylleia Grayi*



in the latter two, some of them are exactly cauline. The behaviour of the leaf trace is mostly similar in *Glaucidium*, *Podophyllum* and *Diphylleia*: some of the leaf trace strands which belong to one foliar leaf enter soon into the pith, but the rest stay in the peripheral parts in every internode as already shown by VAN TIEGHEM (1884, p. 747) in the case of *Podophyllum*. But, in *Hydrastis*, all the leaf trace strands do not enter into the pith in the first internode, but become medullary in the second internode, and the vascular behaviour of this genus is the simplest of four genera. In these genera, medullary bundles appear first at the level of the perianths except in *Hydrastis* which has no medullary bundle in the peduncle.

The floral vascular distribution is the simplest in *Hydrastis*, and most complex in *Glaucidium* in which the perianth is tri- or pentalacunar in the mode of insertion, and the cortical bundles are observed in the upper part of the receptacle. The perianth of *Podophyllum* is tri- or unilacunar and of *Diphylleia* is always unilacunar; the cortical bundles are observed only in the floral axis of *Glaucidium*. The perianth of *Hydrastis* is small and falls off soon as most species of *Thalictrum*; the vascular insertion is unilacunar.

#### 4. HISTOLOGY OF THE AERIAL ORGANS

*Hydrastis*. As far as histology of the genus is concerned, the stem, the peduncle and the floral organs are similar to those of *Glaucidium*, but in *Hydrastis* the cells with somewhat lignified walls are often seen scattered among the cortical elements of the erect stem and of the rhizome; they contain alkaloids.

*Podophyllum* and *Diphylleia*. The aerial organs of these two genera are most closely related to each other, and no histological difference could be found. In both genera, most of the peripheral bundles are, at the basal level of the stem, connected by an interfascicular fibrous cylinder which consists of the layers of several cells with lignified walls (Fig. 17; C, D). Each medullary bundle may be or may not be protected by a group of fibrous cells on the phloem side. Xylem is of a typical V-shape, contrary to that of *Glaucidium* or *Hydrastis*. Endodermis was not distinct.

#### 5. HISTOLOGY OF THE RHIZOME AND ADVENTITIOUS ROOT

##### A. The Rhizome

*Hydrastis*. The outer cortical layers consist often of the cells with lignified walls without forming the typical 'pseudodermis.' The fibres

or fibre-tracheids in groups are not found in the secondary xylem of this genus. In other respects the histological structure of the rhizome is quite similar to that of *Glaucidium*.

*Podophyllum* and *Diphylleia*. The histological studies of rhizomes of *P. peltatum* have been made by HOLM (1899), TISCHLER (1902), of *D. cymosa* by TISCHLER (1902); the author has studied *P. peltatum*, *P. Emodi* and *D. Grayi*.

As regards the structure of the rhizome, *Podophyllum* and *Diphylleia* differ from *Glaucidium* and *Hydrastis* in the following respects:

- 1) The cortical bundles are often found except in *P. Emodi* and *D. Grayi* studied by the author. These bundles have their origin in the vascular strands of the scaly leaves and they fuse to other bundles of the ordinary circle.

- 2) The interfascicular cambium does not differentiate.

- 3) The intrafascicular cambium produces hardly any secondary elements.

- 4) The phellogen is subepidermal in its origin.

It is most remarkable to see that both intra- and interfascicular cambium are very active and produce great amounts of the secondary elements in *Glaucidium* and *Hydrastis*.

#### B. The Adventitious Root

*Hydrastis*. The histological structure is similar to that of *Glaucidium*. Some amounts of the secondary xylem elements are produced by the cambium. The epidermal layer peels off usually in death. The adventitious root produces often the adventitious bud under the ground. This fact is never observed in the other three allied genera.

*Podophyllum* and *Diphylleia*. The secondary xylem elements are never produced in *P. peltatum* and *P. pleianthum* or are produced rather rarely in *P. Emodi* and *D. Grayi*. The epidermal layer peels off in some species, while it does not in other species.

#### 6. DEVELOPMENT AND STRUCTURE OF THE SEEDLING

The seedlings of these four genera show the great morphological and biological peculiarities as already noticed.

The seedlings of *Glaucidium* were studied in detail by the present author, of *Hydrastis* by POHL and HOLM, and of *Podophyllum* by DICKSON (1882) and HOLM.

*Hydrastis*. According to POHL (1894, p. 4) and HOLM (1899, p. 421), there are two developed cotyledons in the first year of its germination, but no other assimilatory organs are usually observed, the plumule



being dormant. The cotyledons are oval in shape without serrations, its petiole being rather short in length. Although the present author was unable to make studies on the seedling of this genus, a word may be appropriately said on the cotyledonary petiole. POHL gave the description with figures of the seedling of *Hydrastis* in 1894. According to his figure (Plate III, Fig. 2), two cotyledonary petioles are free without forming a cotyledonary tube. HOLM (1899, p. 421) mentioned briefly the seedling of *Hydrastis* in his article on *Podophyllum peltatum*, and he described that the cotyledonary petioles of *Hydrastis* are free. It seems rather strange to find that in his paper, HIMMELBAUR (1913, p. 771) described very briefly regarding the petiole of the genus under consideration that "*Hydrastis* hat ausserdem gleich *Podophyllum* zu einem Schlauche verwachsene Keimblätter". He seems to have not consulted POHL's description and figures of *Hydrastis*. Therefore there are inconsistent descriptions on the cotyledonary petiole of *Hydrastis*.

It can be assumed, however, that the cotyledonary petioles can fuse with one another in some seedlings and can be free in other seedlings as in the case of *Anemone fulgens* described by HILDEBRAND (1892; pp. 18-19). Further study is needed regarding this subject.

*Podophyllum*. The author was much interested in finding a great resemblance of the seedling of *P. peltatum* to that of *Glaucidium* in their morphological features and the mode of development. The cotyledonary tube, basal fusion of the cotyledonary margin, short hypocotyl, plumular dormancy:—all of these features are common in both seedlings of the first year of the germination. The only difference between the two is in the shape of the cotyledon; i. e. in *Glaucidium* the cotyledon is oval or elliptical in outline and is entire, while in *P. peltatum* it is somewhat serrated. In the seedlings of the second and the following years, both species have still the tap root, and their monopodial short rhizomes have both three or four scaly leaves and a single petiolated foliar leaf at their top. Some of the differences among the seedlings of the two species are as follows: lamina of *Glaucidium* is three or five lobed and palmate, contrary to that of *P. peltatum* which is peltate; the rhizome of the former genus is somewhat creeping in the ground, whereas that of the latter is quite erect until the rhizome becomes sympodial.

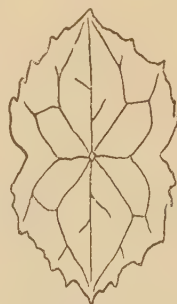


Fig. 18. *Podophyllum pleianthum*. Fused cotyledons. (nat. size)

The seedling of *P. Emodi*, according to DICKSON, LUBBOCK and TISCHLER, has a short hypocotyl and a cotyledonary tube. Its cotyledons are oval in shape, but the basal fusion of the cotyledonary margin does not occur<sup>1)</sup>, and the plumule produces a peltate foliar leaf in the first year, not like the seedling of *P. peltatum*. The author's observation shows that a seedling of *P. pleianthum* cultivated in our Botanic Garden is alike with that of *P. peltatum* in the first year of its germination, particularly in regard to the cotyledonary fusion of basal margin (Fig. 18) and the formation of cotyledonary tube, but in this seedling several foliar leaves appeared in the following year.

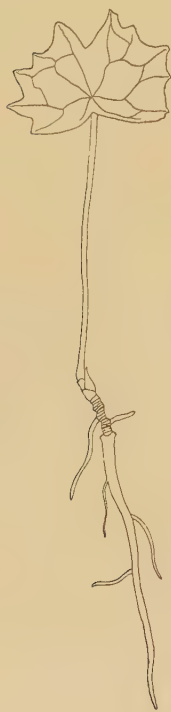


Fig. 19. *Diphylleia Grayi*.  
Seedling after four or five  
years of its germination.  
(nat. size)

*Diphylleia*. An accurate study of the development of the seedling of *Diphylleia* has never been made. According to HIMMELBAUR (p. 755) the seedling has the cotyledonary tube. The author studied the seedlings of *D. Grayi* which were probably in the fourth or fifth year after their germination (Fig. 19). They have three scaly leaves and a petiolated foliar leaf; rhizomes are erect and monopodial, but have no axillary buds. Therefore nothing has been said definitely as to the formation of the cotyledonary tube.

Generally, in the seedlings of these four genera, morphological and biological facts mentioned below are points of interest.

1) The cotyledonary tube is formed in most species. It is found in a few species of Ranunculaceae, Berberidaceae and other dicotyledonous families.

2) In the first year of the germination, the cotyledons represent usually a single aerial organ and the plumule is dormant. This habit is not common to the Angiosperms (VELENOSKÝ; Vol. 2, p. 292).

3) The hypocotyl is usually short.

4) The leaves succeeding the cotyledons are scaly in most species. This feature is, according to HOLM, known only in *Hepatica*, *Asarum*, *Erigenia*, and *Adoxa* among Dicotyledons.

1) In the figure of TISCHLER (p. 114, Fig. 26), the cotyledonary margins seem to fuse to each other at the base, while in that of LUBBOCK (p. 113, Fig. 144), they are quite free.



5) The seedling is extraordinarily slow in its growth and the herb never produces the erect stem within several or more years.

6) In each year the assimilatory organ of the seedling is represented by a single foliar leaf and the other leaves become scaly.

The peculiar habits and structures of these genera seem to be an adaptation to the geophilous life, and it may not be acceptable that the slow growth of the geophilous Angiosperms is *always* caused by the nutritive condition, although one or several foliar leaves of the seedling may often appear abnormally in the first year of the germination in some genera such as *Hydrastis* (POHL, p. 4), *Hepatica* (HILDEBRAND; 1892, p. 39) and *Ficaria* (STERCKX; 1899, p. 43).

#### IV. GENERAL REMARKS AND AFFINITIES

##### 1. HABIT AND GEOGRAPHICAL DISTRIBUTION

*Glaucidium* and *Hydrastis* are monotypic genera,<sup>1)</sup> while *Podophyllum* contains four or more species and *Diphylllea* only two species; all of them are extraordinarily small genera; and their distributions are very limited in the Atlantic coast of North America, and in Eastern Asia as shown in Fig. 20. Especially the former two genera occur in a very limited area.

The distribution of *Glaucidium* extends from the alpine districts of central Japan to Yezo (latitude 36°–44° 30' N.), while *Hydrastis* is found in the Atlantic States of North America (Wisconsin, Missouri, Illinois, Indiana, Kentucky, Pennsylvania, Virginia; latitude 37°–44° N.). It is very interesting to notice that both of them occur almost in the same latitude.

*Podophyllum peltatum* is found more widely distributed than *Hydrastis* in North America; *P. Emodi* at the districts of 3000–5000 meters above sea level in Himalaya, and *P. pleianthum* and *P. versipelle* extend from Himalaya districts through Central China to Formosa.

*Diphylllea cymosa* is found in the east of North America, Central China and Amur, and *D. Grayi* from the alpine districts of central Japan northwards to Sachalin.

*Podophyllum peltatum* grows, according to HOLM, in association with

---

1) Besides *Glaucidium palmatum* SIEB. et ZUCC., two species *G. paradoxum* MAKINO (Bot. Mag. Tokyo; XXIV, p. 71) and *G. pinnatum* FINET et GAGNEPAIN (Bull. Soc. Bot. Fr.; XI, p. 392) were described. But the former is believed as an abnormal specimen of *G. palmatum*, the later species from China is, without doubt, a synonym of *Hylomecon japonicum* PRANTL belonging to Papaveraceae.



Fig. 20. Distribution of *Glaucidium*, *Hydrastis*, *Podophyllum* and *Diphylla*.

G., *Glaucidium palmatum*  
H., *Hydrastis canadensis*  
D.c., *Diphylla cymosa*  
D.G., *D. Grayi*

P.pel., *Podophyllum peltatum*  
P.le., *P. pleianthum*  
P.E., *P. Emodi*  
P.v., *P. versipelle*

*Diphylla*, *Jeffersonia*, *Actaea* and other abnormal Dicotyledons. *Glaucidium* is in association with *Troutvetteria*, *Cimicifuga*, *Diphylla*, *Echinopanax*, etc. at the ground where the author observed it.

Most species of the four genera grow on the mountain sides or in deciduous forests as the undergrowth with other above mentioned geophilous plants, some of which may often be considered morphologically and biologically as somewhat abnormal. This phenomenon was first noticed by HOLM (p. 432), and afterwards by TISCHLER (p. 126). TISCHLER says: "HOLM erkennt völlig die Bedeutung der biologischen Eigentümlichkeiten für die Systematik, wenn er sagt: es besäßen >> *Diphylla*, *Podophyllum*, *Jeffersonia*, *Caulophyllum*, *Actaea*, *Cimicifuga*... ...a number of biological peculiarities that might even lead to a more correct understanding of their true relationship than such small and insignificant floral characters as are used for the establishment of orders. << — Danach könnte man ja Analogieen und Homologieen nicht trennen. Mit HOLM stimme ich darin überein, dass der Systematiker mehr Biologe sein soll als bisher."



The present author supports also the suggestions of HOLM and TISCHLER cited above, and he has no intention of carrying on further discussion of the subject at present.

## 2. AFFINITIES AND CONCLUSION

Now the characteristic features of the four genera must be summarized in order to bring out a clear understanding of the generic relationship.

The following morphological and biological features tabulated (Tables I-III) represent the significant ones of almost all the species among these genera for this purpose.

It is from the data given clear in the tables that *Glaucidium* and *Hydrastis* differ very much more from *Podophyllum* and *Diphylleia* in their features than has hitherto been believed by most authors.

The leaves on the aerial stem are arranged in  $1/2$  divergence in all cases, and the leaves of the geophilous organ show  $2/5$  divergence only in *Podophyllum* and *Diphylleia*, although they are in  $1/2$  divergence in *Glaucidium* and *Hydrastis*. This special occurrence of  $2/5$  phyllotaxis must not be overlooked, because it is usually believed that the  $1/2$  divergence may be derived from  $2/5$  divergence and that the latter shows the original feature in these Dicotyledons.

The tendency of modification of the  $2/5$  phyllotaxis is most clearly manifested in *P. peltatum*: the leaves of a winter bud are attached on the rhizome in  $2/5$  divergence, but they seem to embrace with one another alternately at the higher level and further the cauline leaves are quite opposite. The  $1/2$  phyllotaxis is not common in Ranunculaceae except *Actaea*, *Cimicifuga* and *Anemonopsis*, while the  $1/2$  and  $2/5$  phyllotaxis are equally seen in the Berberidaceous forms.

The elongating mode of rhizome and the structure of the fertile winter bud are the most striking representative features, being distinct in each of the two groups, *Glaucidium-Hydrastis* and *Podophyllum-Diphylleia*. The rhizome similar to that of *Glaucidium* and *Hydrastis* is not usually found in Ranunculaceae. Regular sympodium which elongates horizontally by the dominancy of a definite axillary bud is a significant feature of the rhizome of *Podophyllum* and *Diphylleia*, and this is never found in Berberidaceae or in its allied families. *Caulophyllum* and *Panax* have the rhizomes of the same topography, but the dominant axillary bud changes its position in the winter bud alternately every year, while in the case of the present genera the

TABLE I. EXTERNAL MORPHOLOGY OF ADULT PLANTS

	Number of cauline leaves. Mode of petiole attachment	Inflores- cence	Form of foliar leaf	Phyllo- taxis of leaves in winter bud	Phyllo- taxis of aerial leaves	Mode of rhizomal elongation	Develop- ment of fertile winter bud	Prophyll of axillary bud	Forma- tion of adven- titious bud upon adven- titious root
<i>Glaucidium palmatum</i>	3 (4), alternate	simple	palmate	1/2	1/2	irregular sympodium; not horizontal	an axillary bud conceal- ed becomes aerial after several winters	lateral	not occur
<i>Hydrastis canadensis</i>	2, "	"	"	"	"	"	"	inverted	occur
<i>Iodophyllum pellatum pleioanthum Emodi versipelle</i>	2, opposite 2, " 2(3), alternate 2, "	" cymose — "	peltate " " "	2/5 — — —	1/2 — — —	regular sympodium which elongates in the same direction; horizontal	an axillary bud conceal- ed becomes aerial after two winters	inverted " — —	not occur " — —
<i>Diphylleia cymosa Grayi</i>	2, " 2, "	" "	" "	" "	" "	" "	" "	— lateral	" "

TABLE II. INTERNAL MORPHOLOGY OF ADULT PLANTS

	Number of vascular strands in the basal part of erect stem (number of medullary bundles in parenthesis)	Number of medullary bundles in peduncle	Course of medullary strands in erect stem	Cortical bundles in rhizome	Shape of xylem in stem bundles	Secondary xylem-elements in rhizome	Interfascicular cambium and phellogen	Secondary xylem of adventitious root
<i>Glaucidium palmatum</i>	40-55 (15-25)	5-7	medullary bundles arranged in a circle are leaf trace strands in their origin	not exist	hardly V-shaped	profusely produced	interfascicular cambium very active	formed
<i>Hydrastis canadensis</i>	25-30 (4-5)	0	"	"	"	"	"	"
<i>Podophyllum peltatum</i>	60-70 (30-35)	3-6	medullary bundles scattered; some at the centre cauline	exist	V-shaped	not produced	interfascicular cambium does not appear; phellogen subepidermal	not formed
<i>pleianthum</i>	—	—	—	—	—	—	—	—
<i>Emodi versipelle</i>	—	—	—	—	—	"	"	slightly formed
	—	—	—	—	—	—	—	not formed
<i>Diphylleia cymosa</i> Gray	60-70 (30-40)	3-4	—	" not exist	—	—	—	—
			"		"	"	"	sometimes formed



TABLE III. SEEDLING MORPHOLOGY

	Cotyledonary petiole	Plumule in the first year of germination
<i>Glaucidium palmatum</i>	fused	dormant
<i>Hydrastis canadensis</i>	free (POHL) fused (HIMMELBAUR)	"
<i>Podophyllum peltatum pleianthum Emodi versipelle</i>	fused " "	dormant one foliar leaf is produced "
<i>Diphylleia cymosa Grayi</i>	fused (HIMMELBAUR) —	— —

(— denotes the data not observed by any author)

dominant axillary bud occupies a constant position in the winter bud of each year.

The mode of ramification observed in the two genera under consideration may be an adaptation to the geophilous life. For this reason their rhizomes are in the same depth of the ground, occupying much more area and avoiding the entanglement of rhizomes.

The inverted prophyll is probably found in *Hydrastis*, *Podophyllum peltatum* and *P. pleianthum*, and these are one of the prominent characteristics in Monocotyledons and Polycarpiceae, while *Glaucidium* and *Diphylleia Grayi* belonging to the latter have lateral prophylls, which are prevalent in most of the Dicotyledons.

Vascular bundles of the aerial stem are quite irregularly scattered in *Podophyllum* and *Diphylleia*, while in *Glaucidium* and *Hydrastis* they are arranged nearly in two circles. The medullary bundles are usually leaf trace strands in *Glaucidium* and *Hydrastis*, but some of them are cauline in *Podophyllum* and *Diphylleia*. The medullary bundles occur in floral receptacles of these genera, except in *Hydrastis*, but do not in most species of Ranunculaceae or of Berberidaceae. The floral vascular distribution is most complex in *Glaucidium*.

The V-shape of xylem is usually found in the aerial stem of Ranunculaceae and of other allied groups in Dicotyledons, but not in *Glaucidium* and *Hydrastis*.

In short, the four genera are represented by two types, i.e. *Glaucidium-Hydrastis* and *Podophyllum-Diphylleia* types as suggested by other authors. Judging from the vascular distribution and histology of adult plants and also from the features of seedlings, *Glaucidium* seems to be a much more specialized genus than *Hydrastis*. HIMMELBAUR (pp. 755-756) assumed that the genus *Diphylleia* may be the mother form from which *Podophyllum* is derived, in considering various facts such as the rhizome of 2/5 phyllotaxis, the stem structure, the feature of pedicel, number of species included in one genus, and the geographical distribution, but the author could find no good reasons to support his conclusion in the present study.

Also from the standpoint of the chromosome morphology, MIYAJI (1927, p. 569) showed that the genus *Glaucidium* has not any relationship with any other members of Ranunculaceae, and further LANGLET (1928, p. 180) proposed to group *Glaucidium* and *Hydrastis* under Podophylloideae, one of the Berberidaceous subfamilies with two genera *Podophyllum* and *Diphylleia*.

According to the author's study, *Glaucidium-Hydrastis* type deviates much more from the representatives of Ranunculaceae, and *Podophyllum-Diphylleia* type also from those of Berberidaceae than has hitherto been accepted; and the two types are quite clearly distinguished from each other by the morphological and biological features, even if the floral structure, which is of the most significance for the systematists, is not taken into consideration. These morphological and biological gaps between the two types seem to be as large as the gaps between *Podophyllum-Diphylleia* type and some herbaceous representatives of Berberidaceae such as *Achlys*, *Jeffersonia*, *Epimedium*, *Caulophyllum*, etc.

Taking above mentioned facts into consideration, the author is of the opinion that these four genera *Glaucidium*, *Hydrastis*, *Podophyllum* and *Diphylleia* may be excluded from both Ranunculaceae and Berberidaceae, and that these genera form the family Podophyllaceae, into which two tribes Podophylloideae and Glaucidioideae are to be taken, although Glaucidioideae was included by HIMMELBAUR (p. 788) in Berberidaceae. The Podophyllaceae introduced by TISCHLER (p. 130) did not comprise *Glaucidium* and *Hydrastis*.

Apart from the considerations of the systematic relationship, the morphological and biological features of the plant groups treated in this paper may, in further studies, give some suggestions for the evolution of the geophilous habit of Angiosperms.

## V. SUMMARY

1. The monotypic genus *Glaucidium* was studied both morphologically and biologically.

a. On the aerial stem and rhizome, the leaves are arranged in  $1/2$  divergence. An axillary bud in the winter bud becomes aerial after several winter seasons, and the rhizome is represented by the irregular sympodium, showing a massive appearance.

b. In the seedling of the first year of the germination, cotyledonary petioles are fused with each other, forming a cotyledonary tube; and two cotyledons fuse also at their basal margin. Plumule is dormant. In the successive years, the seedling has three or four scaly leaves and a single foliar leaf. The seedling features of this genus are remarkably similar to those of *Podophyllum peltatum*.

c. A circle of the medullary bundles is observed from the base of the erect stem upwards to the floral receptacle; the origin and the behaviour of these medullary bundles were traced. Cortical bundles are observed in the floral receptacle.

2. *Glaucidium*, *Hydrastis*, *Podophyllum* and *Diphylleia* were compared with one another both morphologically and histologically.

a. Erect stems of all the genera have a few foliar leaves which are arranged in  $1/2$  divergence. Scaly leaves of the geophilous organ are arranged in  $1/2$  divergence and foliar leaves are palmate in *Glaucidium* and *Hydrastis*, while scaly leaves are in  $2/5$  divergence and the foliar leaves are peltate in *Podophyllum* and *Diphylleia*.

b. *Glaucidium* and *Hydrastis* have the rhizomes of irregular sympodium, and an axillary bud in the winter bud becomes aerial after several winter seasons. *Podophyllum* and *Diphylleia* have the horizontal rhizomes of sympodium which elongate in the same direction as the older part of the rhizome as if it were the main axis itself. An axillary bud in the winter bud becomes aerial after two winters.

c. Medullary bundles of *Glaucidium* and *Hydrastis* are arranged in a single circle and are leaf trace in their origin, while those of *Podophyllum* and *Diphylleia* are scattered irregularly in the pith, and some of them are cauline.

d. Xylem of the erect stem is V-shaped in *Podophyllum* and *Diphylleia*, while it is hardly V-shaped in *Glaucidium* and *Hydrastis*.

e. The intra- and interfascicular cambium of rhizomes and the cambium of adventitious roots are very active in *Glaucidium* and



*Hydrastis*, producing secondary xylem elements, while they are never or hardly active in *Podophyllum* and *Diphylleia*.

f. The cotyledonary tube is usually formed in the seedlings of these four genera, and the plumule of most species is dormant in the first year of the germination. The seedling produces, as usual, several scaly leaves and a single foliar leaf every year, and the development of the seedling is extraordinarily slow.

3. From the morphological and histological points of view, the *Glaucidium-Hydrastis* type is quite clearly distinguished from the *Podophyllum-Diphylleia* type. *Glaucidium* and other three genera mentioned above may be excluded from both Ranunculaceae and Berberidaceae, and may now constitute the family Podophyllaceae which are to be divided into two tribes, i. e. Podophylloideae, including *Podophyllum* and *Diphylleia*, and Glaucidoideae, including *Glaucidium* and *Hydrastis*.

In conclusion, the author desires to express his sincere thanks to Professor Y. OGURA for his kind criticism and valuable advice. Thanks are also due to Professor T. NAKAI for his helpful suggestion.

April, 1930

Botanical Institute, Faculty of Science,  
Imperial University of Tokyo

## VI. LITERATURE

- BAILLON, H. (1868) Monographie des Renonculacées. Paris.  
BASTIN, E. S. (1894) Structure of *Podophyllum*. Amer. Journ. Pharm. Vol. 66.  
BOWERS, H. (1891) A contribution to the life-history of *Hydrastis canadensis* L. Bot. Gaz. Vol. 16.  
CITERNE, P. E. (1892) Berbéridéés et Erythrospermées. Thèse Paris.  
DE BARY, A. (1877) Vergleichende Anatomie der vegetativen Organe der Phanerogamen und Farne. Leipzig.  
DICKSON, A. (1882) On the germination of *Podophyllum Emodi*. Transact. Bot. Soc. Edinburgh. Vol. 16.  
DOULIOT, H. (1889) Recherches sur le périoderme. Ann. Sci. nat. Sér. 7, Bot. Tom. 10.  
ENGLER, A. & K. GILG (1924) Syllabus der Pflanzenfamilien. 9 u. 10 Aufl. Berlin.  
GATIN, V. C. (1920) Recherches anatomiques sur le pédoncule et la fleur des Liliacées. Rev. gen. Bot. Tom. 32.

- HILDEBRAND, F. (1892) Einige Beobachtungen an Keimlingen und Stecklingen. Bot. Zeit. Bd. 50.
- HIMMELBAUR, W. (1913) Die Berberidaceen und ihre Stellung in System. Eine phylogenetische Studie. Denkschr. mathem.-naturwiss. Kl. Bd. 89.
- HOLM, T. (1899) *Podophyllum peltatum*, a morphological study. Bot. Gaz. Vol. 16.
- HUTH, E. (1892) Revision der kleineren Ranunculaceen-Gattungen *Myosurus*, *Trautvetteria*, *Hamadryas*, *Glaucidium*, *Hydrastis*, *Eranthis*, *Coptis*, *Anemonopsis*, *Actaea*, *Cimicifuga* und *Xanthorrhiza*. Bot. Jahrb. Bd. 16.
- KUMAZAWA, M. (1930) Studies on the structure of Japanese species of *Ranunculus*. Journ. Fac. Sci. Imp. Univ. Tokyo. Sec. 3, Bot. Vol. 2, Part 3.
- LANGLET, O. F. (1928) Einige Beobachtungen über die Zytologie der Berberidaceen. Svensk Bot. Tidskr. Vol. 22.
- LOTSY, J. P. (1911) Vorträge über botanische Stammesgeschichte. Bd. 3. Jena.
- LUBBOCK, J. (1892) A contribution to our knowledge of seedlings. Vol. 1. London.
- MIYAJI, K. (1927) Über die somatischen Chromosomen einiger Ranunculaceen. (japanisch) Bot. Mag. Vol. 41.
- POHL, J. (1894) Botanische Mitteilung über *Hydrastis canadensis* L. Bibl. Bot. Bd. 29.
- PRANTL, K. (1887) Beiträge zur Morphologie und Systematik der Ranunculaceen. Bot. Jahrb. Bd. 9.
- SCHUMANN, K. (1897) Die Morphologie einiger Drogen. Arch. Pharm. Bd. 235.
- SOLEREDER, H. (1899) Systematische Anatomie der Dicotyledonen. Stuttgart.
- (1908) Ergänzungsband zur systematische Anatomie der Dicotyledonen. Stuttgart.
- STERCKX, R. (1899) Recherches anatomiques sur l'embryon et les plantules dans la famille des Renonculacées. Arch. Inst. Bot. Univ. Liège. Vol. 2.
- TISCHLER, G. (1902) Die Berberidaceen und Podophyllaceen. Versuch einer morphologisch-biologischen Monographie. Habilitationsschrift. Leipzig.
- VAN TIEGHEM, P. (1884) Traité de botanique. Paris.
- VELENOVSKÝ, J. (1907) Vergleichende Morphologie der Pflanzen. Teil 2. Prag.
- WETTSTEIN, R. (1924) Handbuch der Botanik. 3 Aufl. Leipzig und Wien.



# JOURNAL OF THE FACULTY OF SCIENCE IMPERIAL UNIVERSITY OF TOKYO

## SECTION I. MATHEMATICS, ASTRONOMY, PHYSICS, CHEMISTRY

Vol. I, Completed.

Vol. II, Part 1. Z. Suetuna, Über die Anzahl der Idealfaktoren von  $n$  in einem algebraischen Zahlkörper. Price ¥ 0.60

" Part 2. K. Shoda, Über die Automorphismen einer endlichen zerlegbaren Gruppe. Price ¥ 0.60

## SECTION II. GEOLOGY, MINERALOGY, GEOGRAPHY, SEISMOLOGY

Vol. I, Completed.

Vol. II, Completed.

Vol. III, Part 1. B. Kotô, The Iwatsuki Seismic Zone as a Factor of the Habitual Tokyo Earthquake. B. Kotô, The Physiographic Division of Pacific North America.

Price ¥ 1.00

" Part 2. N. Nasu, A Stereometrical Study of the Aftershocks of the Great Tango Earthquake with Special Reference to the Mechanism of their Occurrence.

Price ¥ 1.90

## SECTION III. BOTANY

Vol. I, Completed.

Vol. II, Part 1. G. Yamaha, Experimentelle zytologische Beiträge. I. Mitteilung. Orientierungsversuche an den Wurzelspitzen einiger Pflanzen. Price ¥ 4.60

" Part 2. G. Yamaha, Experimentelle zytologische Beiträge. II. Mitteilung. Über die Wirkung des destillierten Wassers auf die Wurzelspitzenzellen von *Vicia Faba* bei verschiedenen Temperaturen. Price ¥ 1.60

" Part 3. M. Kumazawa, Studies on the Structure of Japanese Species of *Ranunculus*. Price ¥ 1.00

" Part 4. M. Kumazawa, Morphology and Biology of *Glaucidium palmatum* Sieb. et Zucc. with Notes on Affinities to the Allied Genera *Hydrastis*, *Podophyllum* and *Diphleia*. Price ¥ 0.60

## SECTION IV. ZOOLOGY

Vol. I, Completed.

Vol. II, Part 1. Y. Okada, On the Development of a Hexactinellid Sponge, *Farrea Sollasi*. T. Kamada, Current Strength and Anodal Galvanotropism in *Paramecium*.

T. Kamada, The Time-Intensity Factors in the Electrodestruction of the Membrane of *Paramecium*. Price ¥ 1.70

" Part 2. T. Goda, Cytoplasmic Inclusions of Amphibian Cells with Special Reference to Melanin. T. Kamada, Control of Galvanotropism in *Paramecium*. Price ¥ 2.30

## SECTION V. ANTHROPOLOGY

Vol. I, Part 1. A. Matsumura, On the Cephalic Index and Stature of the Japanese and their Local Differences. A Contribution to the Physical Anthropology of Japan.

Price ¥ 11.00



## CONTENTS

M. KUMAZAWA:—Morphology and Biology of *Graucidium palmatum* SIEB. et ZUCC. with Notes on Affinities to the Allied Genera *Hydrastis*, *Podophyllum* and *Diphylleia* . 345

---

This JOURNAL is on sale at

MARUZEN CO., LTD.

6, Nihonbashi Tori-Nichome, Tokyo

R. FRIEDLÄNDER & SOHN

Karlstr. 11, Berlin, N.W. 6

---

Price in Tokyo: Yen 0.60 for this Part

---

昭和五年七月二十九日印刷  
昭和五年七月三十一日發行

編纂兼發行者

東京帝國大學

印刷者 東京市深川區東大工町四十八番地  
星野錫

印刷所 東京市深川區東大工町四十八番地  
東京印刷株式會社

賣捌所 東京市日本橋區通二丁目六番地  
丸善株式會社